Remote Sensing of Environment 182 (2016) 90–98

Contents lists available at ScienceDirect

Remote Sensing of Environment

journal homepage: www.elsevier.com/locate/rse

Leaf flush drives dry season green-up of the Central Amazon

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ARTICLE INFO

Article history:
Received 12 August 2015
Received in revised form 30 April 2016
Accepted 15 May 2016
Available online 24 May 2016

Keywords:
Tropical forest
Dry season green-up
Enhanced Vegetation Index
Phenocam
Green Chromatic Coordinate
Leaf flush
Leaf abscission

ABSTRACT

Understanding how land surface seasonality emerges from individual tree crown phenology is a key challenge of tropical ecology. We used daily images over a full year from a tower-mounted RGB camera to quantify the leaf phenology of 267 individual tree crowns in an evergreen Central Amazon forest. The Green Chromatic Coordinate, an index of each crown's greenness, showed rapid large-amplitude positive and negative changes, each generally occurring once per year. Rapid increase was attributed to leaf flushing and occurred in 85% of all crowns. Rapid negative change occurred in 42% of individuals, caused mostly by massive pre-flush leaf abscission (31% of all crowns). Flushing was concentrated in the five driest months (55% of crowns) compared to the five wettest months (10%). Inter-crown variance of greenness was lowest in the wet season when fewer crowns were abruptly abscising or flushing leaves. With a one month lead, flushing frequency closely tracked seasonal light availability ($R = 0.89$) and was inversely correlated with rainfall ($R = -0.88$). We linked the post-flush age of each crown's leaf cohort to the Enhanced Vegetation Index (EVI) of crowns at different phenostages on a nadir view QuickBird image. When aggregated to landscape-scale, this camera-based EVI closely followed ($R = 0.95$) the MODIS MAIAC EVI of the same site, fully corrected for sun-sensor geometry effects. Leaf phenology therefore drives the dry season green-up detected by MODIS in the Central Amazon. It is also consistent with evolutionary strategies to couple photosynthetic efficiency with light availability and to avoid predation and disease on vulnerable young leaves.

1. Introduction

The response of Amazon forest phenology to seasonal precipitation, as detected by the Moderate Resolution Imaging Spectroradiometer (MODIS), has been a subject of debate (Galvão et al., 2011; Huete et al., 2006; Maeda, Heiskanen, Aragão, & Rinne, 2014; Morton et al., 2014; Saleska, Didan, Huete, & da Rocha, 2007; Saleska et al., 2016; Samanta, Ganguly, and Myneni, 2011; Xiao et al., 2005; Xiao, Hagen, Zhang, Keller, & Moore, 2006). Enhanced Vegetation Index (EVI) derived from some MODIS products, such as MOD09A1 and the MOD13 group, is not corrected for the effects of view and solar angles. View angle effects have no seasonal trend in time series and were effectively removed in an early report of dry season green-up (Huete et al., 2006) by averaging over very large sample areas. Solar zenith angle, however, does have a trend during the Central Amazon's drier months of June to September. This trend is not removed in the standard Nadir BRDF Adjusted Reflectance (NBAR) products (MCD43A4, MCD43B4), for which solar zenith angle is adjusted to local noon. From the June solstice to the September equinox, the solar zenith angle at local noon (and at the fixed times of MODIS platform passages) decreases in the Central Amazon, leading to a progressive reduction in sub-pixel shadow fraction and consequent increase in NIR reflectance and EVI (Galvão et al., 2011; Morton et al., 2014). Consequently, an apparent dry season green-up is expected in uncorrected and in NBAR-corrected products, even in the absence of true phenological causes, such as increase in total leaf area or flushing new leaves free of epiphylls (Toomey, Roberts, & Nelson, 2009; Wu et al., 2016).

Bi et al. (2015); Guan et al. (2015) and Maeda et al. (2014) have recently shown that, after fully correcting for both view and solar angle, a dry season increase in EVI is still detectable in the Central Amazon. This true dry season green-up between June and October is about one half that of uncorrected EVI, though still well above the noise level of the data (Guan et al., 2015; Saleska et al., 2016).

Independent evidence for seasonal change in Central Amazon canopy greenness is clearly relevant to this debate. An attractive alternative

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http://dx.doi.org/10.1016/j.rse.2016.05.009
0034-4257/

is to monitor the upper canopy with tower-mounted cameras, or phenocams. These provide very high temporal frequency, useful for controlling lighting artifacts. By combining seasonal monitoring of crown-level leaf phenology stages from tower-mounted RGB phenocams with the EVI values of these same phenostages recognized in the true-color RGB space of high resolution orbital sensors that also have an NIR band, it is possible to derive the seasonal pattern of Central Amazon EVI at the landscape scale.

The study of temperate forest phenology using phenocams is well advanced (Hufkens et al., 2012; Richardson, Braswell, Hollinger, Jenkins, & Ollinger, 2009; Richardson et al., 2007; Sonnentag et al., 2012), though still improving (Yang, Tang, & Mustard, 2014). The landscape-scale annual phenological signal of a tropical evergreen forest is much more subtle than that of a deciduous temperate forest, so that lighting artifacts constitute a larger fraction of detected change. Furthermore, leaves of different ages for the same species exhibit different colors in the visible spectrum (Toomey et al., 2009; Yang et al., 2014) so that greenness indicators derived from RGB cameras are not directly correlated with leaf amount.

Here we describe the leaf phenology of a primary forest at a Central Amazon site using a full year of daily images from an RGB camera mounted ~50 m above the upper canopy. We ask the following questions:

(1) What are the seasonal patterns of leaf renewal in the upper canopy at the crown and landscape scales?
(2) Is Central Amazon leaf phenology consistent with seasonal change in the EVI detected with the MODIS satellite?

To answer our first question we develop and apply digital methods that detect very rapid changes in leaf age and amount within a crown, while minimizing artifacts related to more gradual leaf color change of mature healthy leaves, seasonal variation in light quality and instrument errors. Visual and digital detections are compared to evaluate accuracy. We also compare the monthly frequencies of rapid leaf phenology changes with monthly precipitation, photosynthetically active radiation (PAR) and soil moisture. Our second question is addressed by relating the post-flush ages of leaf cohorts in the tree crowns seen from the tower to the EVI of crown phenostages obtained from a nadir-view QuickBird image. We close with a discussion of evolutionary drivers of leaf phenology in the Central Amazon.

2. Methods

2.1. Study area and camera details

We studied an upland forest on a well-drained clay-soil plateau 150 km northeast of Manaus, Brazil, at the Amazon Tall Tower site (59.0005°W and 2.1433°S). About 600 trees and >140 tree species are found in a typical hectare (Andreae et al., 2015). The most abundant families are Lecythidaceae, Sapotaceae, Leguminosae, Burseraceae, Euphorbiaceae and Lauraceae.

We monitored the upper canopy leaf phenology from 01 July 2013 to 30 June 2014, with an RGB Stardot Netcam model XL 3MP (2048 × 1536 pixels) mounted 81 m above the ground and ~50 m above the forest canopy. The camera was controlled by a Compulab model Fit-PC2i microcomputer with heat-resistant solid-state drive. All components were installed inside weather- and insect-resistant boxes with thermal shielding and passive ventilation. The camera box was fitted with an acrylic window cleaned every four months. The camera view was west (270°), always monitoring the same crowns and excluding the sky (Fig. 1a). A 96° wide-angle lens and the high vantage point provided coverage of four hectares. Automatic exposure was turned on and automatic color balance turned off. The camera and the computer automatically rebooted and reestablished communication and settings after power losses.

2.2. Greenness metric and detection of phenostages

Greenness as used here is the Green Chromatic Coordinate of a pixel, or g_{cc} (Richardson et al., 2007; Woebbecke, Meyer, Von Bargen, & Mortensen, 1995), defined as the fractional contribution of the green channel's digital brightness value to the summed brightness values of all three RGB channels. While the g_{cc} of pixels in a leafless crown is lower than the g_{cc} of a fully leafy crown, "greenness" as measured by g_{cc} is not a direct measure of leaf amount of a crown, because g_{cc} also changes with leaf color. Gradual change in leaf color with age presents a challenge for measurement of seasonal change in landscape-scale leaf amount of a tropical forest using only RGB spectral bands.

Nonetheless, a large abrupt increase in the g_{cc} timeline of a single crown can only indicate rapid production of a new light-green leaf cohort in that crown. A large and abrupt decrease in g_{cc} within a single crown can be safely attributed to either rapid leaf loss toward a

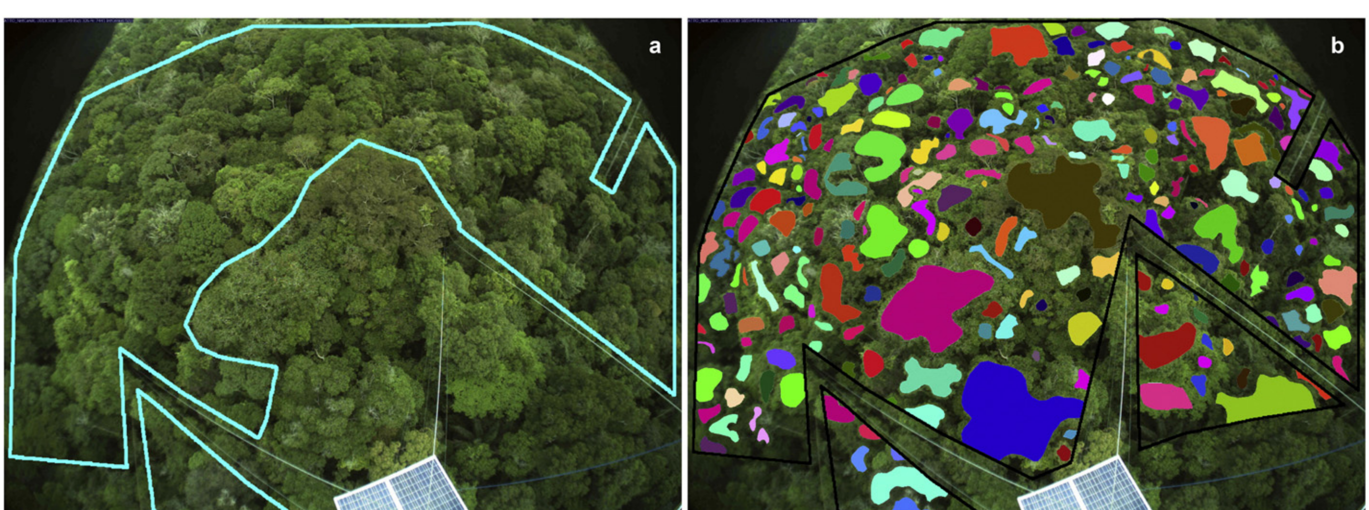

Fig. 1. Regions of interest used in digital analysis. The image area covers approximately four hectares. Radiometric intercalibration to a single reference date used the large forest area outlined in (a); corrected daily values of Green Chromatic Coordinate were then obtained for each of 267 individual crowns shown in (b).